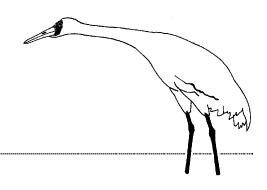
# Genetic Management

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ue to the trends toward extinction of many crane species in the wild, the continued development of cooperative management programs for captive cranes is a critical component of recovery strategies.

Significant progress has been made in the last ten years toward the improvement of techniques for preserving genetic diversity. Successful regional programs are under development and cooperation within regions is increasing. It is now important to develop mechanisms for coordination between these regions toward world conservation strategies. New research is needed to evaluate and refine management programs.

Efforts to preserve endangered species should promote self-sustaining wild populations. The establishment of captive "species banks" can be critical to ensure the survival of some species, and to promote the preservation of genetic diversity so populations are able to respond to change (Mettler and Gregg 1969; Wilcox et al. 1986). Lack of diversity often reduces resistance to disease, decreases fertility, increases embryo mortality, and reduces growth rates (Frankel and Soule 1981).

This chapter discusses the management of genetic diversity in captive populations of cranes. We present the basic principles and tools of genetic and demographic management of small captive populations, and review cooperative management programs and useful contacts. Finally, we summarize genetic research needs and projects underway.

## Genetic and Demographic Management

Every individual in a population represents a unique combination of alleles (alternative forms of a gene). The population itself, however, can be described by measuring the **frequency of each allele** at each locus. Some alleles will be common, shared by most of the

population's members; other alleles will be rare, found in only a few animals. The object of captive management is to preserve, so far as is possible, the genetic description of the wild population—to preserve the highest diversity possible. Achieving this goal requires controlled propagation.

Any single non-inbred individual represents 50% of the total genetic diversity in a population (Denniston 1978). However, the alleles in oneanimal do not represent the distribution of alleles in the population, unless that population contains essentially no variability. A captive population founded by only a few individuals maylack rare alleles or over represent them. The larger the number of individuals contributing to a captive population, the more accurately total genetic diversity of the species will be represented. The genetic diversity represented, however, does not increaselinearly with thenumber of contributing individuals. In theory, the largerthe number of wildindividuals used to start the captive population, the better. In practice, captive managersare constrained by the lack ofindividuals of rare species, a lack of space, and frequently by the characteristics of existing captive populations. These populationsmay contain animals of unknown origins or inbred individuals and have suboptimal distributions of age, sex, and parentage.

A population's genetic diversity is only partly dependent upon its actual size, N. The effective genetic size of a population is estimated by its **effective population number**, N<sub>e</sub> (Crow and Kimura 1970). N<sub>e</sub> measures the way in which the population reproduces, transmitting its genes to the next generation (Foose and Ballou 1988). Specifically, N<sub>e</sub> is the number of individuals that would be required in a hypothetical, random breeding population of constant size, equal sex ratio, and with non-overlapping generations to retain the same amount of genetic diversity as was retained in the original population.

Ne increases when: (1) the number of breeders increases, (2) the number of offspring per breeder increases, (3) the number of offspring per breeder becomes more equal (the variance in the number of

offspring per breeder decreases [Frankel and Soule 1981]), and (4) the sex ratio is even (at least in most species). Populations with larger N<sub>e</sub> values loose genetic diversity and rare alleles more slowly than populations with smaller N<sub>e</sub> values (Denniston 1978). When N<sub>e</sub> reaches a certain size, somewhere around 500 animals, the population may gain genetic variation when the rate of mutation exceeds genetic drift (Frankel and Soule 1981).

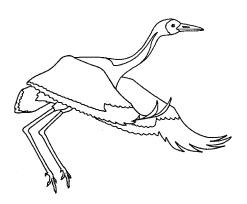
The first priority of genetic management is to breed as many of the founders in a population as possible.  $N_e$  is linearly related to the number of founders in the population. A **founder** is usually defined as an animal that is taken from the wild and has no relatives in captivity except its own descendants. Potential founders that die without leaving offspring contribute nothing to the gene pool unless their genetic material has been cryopreserved in a way that allows them to produce offspring later.

Thenextpriorityisto increasethenumberof **offspring perfounder**. Quicklybreeding a rare speciesisimportantto increase itschances oflongterm survival(Soule 1983) andisgeneticallybeneficial as well(Flesness 1977). However, skewing thegenetic representationinfavor of a few founderstoachieve this growth can be harmful. Also, fluctuations in growthratesshouldbe avoidedbecausethey canskew theagedistribution(seebelow)andthereby decrease thepopulation's stability. Programmanagersmust also determinesize of a minimum viable population (MVP).MVP can be estimated using CAPACITY software (see Studbook section below). The carrying capacity for thispopulationincaptivity needstobe equalorlarger thantheMVP toachieve program goals.

Once a captive population is large enough to withstand extinction, it should be managed to equalize the genetic representation of its founders. Increasing the number of offspring of poorly represented pairs can dramatically increase the genetic diversity of a population without increasing the number of individuals (Denniston 1978; Swengel 1987). Sometimes this also requires curtailing breeding or culling offspring for highly represented pairs.

Culling involves dispersing cranes or euthanasia. If a captive population is at carrying capacity, N<sub>e</sub> can be increased by culling offspring of over-represented lineages. Culling can thereby correct some of the genetic harm due to unequal breeding or differential survival. Generally, only second or subsequent generation animals are culled.

The genetic diversity of a population is greatest when each founder has the same number of offspring. When each pair has the same number of chicks, N<sub>e</sub> is twice that of a random breeding population (Crow and Kimura 1970; Frankel and Soule 1981). Captive crane pairs generally have very unequal numbers of chicks (Swengel 1987; Sheppard 1988) (N<sub>e</sub><N). Long reproductive life spans also enable a few pairs to produce most of the next generation.



Demographic management involves the examination and manipulation of population characteristics toward achieving stable age structure and a stable population size near carrying capacity. Age specific fertility and age specific mortality are the most important data. Demographic analysis reveals the number of offspring required from each breeding-age crane to maintain a stable population. Managers must also know the age at first reproduction, longevity, reproductive life span, and sex ratio before enacting long-term demographic management. From this information, mathematical models aided by the computer (see Studbook section below) can predict population growth and the rate of loss of genetic material. Such models establish numbers of offspring needed per pair (Odum 1994). Lifetime reproductive goals can then be translated into annual breeding objectives for each bird.

Optimally, the sex ratio for captive crane populations should be even. Some captive populations have uneven sex ratios. For example, in the past, Redcrowned Cranes in North America have been skewed toward females and Siberian Cranes toward males. This skewing is probably an artifact of small population size.

During each generation, some genetic diversity is lost because each parent contributes only half of its genes to an offspring. On average, it requires six offspring to represent 98.4% of each parent's genetic

information. To reduce therate of lossof genetic diversity, it is important to maximize generation time (the average age at which anindividual produces offspring). One possible strategy for a population near carrying capacityis to allow each pairto breedonce or twice when they reach sexual maturity toensure retention of some genetic information of the breeders. Then allow the pairto produce only one offspring every five years until the desired number of offspring are produced. An alternate strategy is to delaybreeding, cull olderoffspring, and breed the youngest offspring.

**Inbreeding**, the breeding of genetically related individuals, decreases heterozygosity (proportion of loci measured which have two different alleles), increases homozygosity (proportion of loci measured which have the same alleles), and is generally harmful (Flesness 1977; Frankel and Soule 1981; Ralls et al. 1988). Inbreeding reduces fertility and hatchability in Red-crowned Cranes (Swengel 1985), leads to greater expression of the population's genetic load (i.e., increases the rate of expression of harmful recessive alleles), and decreases population fitness especially for reintroductions (Frankham et al. 1986). Some alleles influence survival and fitness more than others. It may be possible to design breeding programs to prevent the loss of highly advantageous alleles. Flesness (1977) describes how to avoid inbreeding. Inbreeding coefficients for all potential pairings can be obtained using SPARKS and GENES software (see Studbook section below).

Populations which go through a genetic bottleneck (i.e., major reduction in size), and are therefore derived from a few individuals, are more likely to be at greater risk for expression of genetic load through inbreeding. Because we normally cannot assess the number of deleterious genes in the founding individuals, it is best to avoid unnecessary inbreeding. Bottlenecks also result in the loss of allelic and gene diversity (related to, but not the same as heterozygosity), which estimate the presence of rare alleles. This loss decreases the ability of the population to adapt to changes in its environment (Mettler and Gregg 1969). Breeding strategies should be designed to preserve three types of genetic diversity: heterozygosity, allelic diversity, and gene diversity (Willis and Wiese 1995).

In captive breeding programs, it is important to avoid artificial selection (Miller and Hedrick 1991). We should not select for birds adapted to captivity (e.g., tame birds are often more productive). Natural selection has selected favorable traits for millions of years, and the best we can do is minimize evolutionary

change while the birds are in captivity. Geneticists debate the use of artificial selection to reduce genetic load. Frankham et al. (1986) recommend preventing cranes with harmful traits from breeding. Natural selection after release will remove harmful traits, so artificial selection is generally avoided.

To aid readers, a summary of guidelines to maximize genetic diversity is presented in Table 9.1. Table 9.2 summarizes procedures for selecting mates and targeting the number of offspring per pair.

### Studbooks

The studbook, the basic tool for genetic management, contains a genealogy of all animals living or dead (see Table 9.3 for studbook managers, and Table 9.4 for a sample studbook). Although several species have international studbooks, regional studbooks also are kept to facilitate local management decisions.

Each studbook contains identification numbers, date of hatch, sex, parentage, date and cause of death, and dates and locations where the cranes have been

#### **TABLE 9.1.**

#### Summary of genetic and demographic management guidelines to maximize genetic diversity.1

- Start the population with an adequate number of founders (at least 20 founders which effectively reproduce).
- 2. Expand the population to captive "carrying capacity" as quickly as possible. Carrying capacity should be larger than the minimum viable population size.
- 3. Equalize the sex ratio (number of breeding males: number of breeding females).
- 4. Equalize family size (the breeding animals should have equal numbers of offspring contributing to the next generation).
- Stabilize the size and growth rate of the captive population once it reaches "carrying capacity" (generally 100-500 cranes). Avoid fluctuations in population size.
- 6. At this stage, manage for longer generation times.
- 7. Minimize inbreeding at all stages.
- 8. Manage for stable age structure at all stages.

<sup>&</sup>lt;sup>1</sup> Adapted from DeBoer (1989).

#### **TABLE 9.2.**

## Recommended procedures for selecting mates and targeting number of offspring per pair.<sup>2</sup>

- Assign genetic values to birds. (GENES software provides an ordered list of mean kinship by sex and a measure of rare alleles in the "proportion of genome unique" report.)
- First, breed birds with highest genetic value (lowest mean kinship). These birds should produce the largest number offspring.
- Second, breed birds with lower genetic value, but whose alleles may be lost soon. (Knowledge of managers and kinship value in the SPARKS masterplan report are sources of this information.)
- 4. Pair individuals according to the following criteria:
  - Mate individuals with similar genetic value (e.g., mean kinship) to avoid combining rare and common alleles.
  - b. Mate individuals whose offspring will have low inbreeding coefficients.
  - Maximize pairing success based on age, behavior, and physical condition.
  - d. Adjust for logistical considerations such as transfers, quarantine, and cost.
  - e. Adjust, if needed, based on wishes of individuals or institutions.

held. It also includes mates, inbreeding coefficients, living offspring and siblings, and summary tables of holdings by institution, births, deaths, and transfers. Some detail may also be given on status in the wild and captive management efforts.

A studbook-like report for species which do not have an official studbook can now be provided by the International Species Information System (ISIS) (see Chapter 10). ISIS has developed a valuable new software program entitled Single Population Analysis and Record Keeping System (SPARKS). This software is designed for the production of studbooks and to conduct basic genetic and demographic analysis on population data. Supporting software (GENES, DEMOG, and CAPACITY) provides for most of the analysis described in this section. Individuals and institutions with captive cranes are encouraged to join ISIS. Further information can be obtained by contacting ISIS (address in Appendix) or ICF.

## Cooperative Captive Management Programs

Considerable effort has been focused, both regionally and internationally, on coordinating captive management efforts to preserve genetic diversity. For these programs to succeed, individual animals must be paired and bred (or not bred) according to genetic and demographic management strategies. To a degree, participating institutions have less autonomy in determining the fate of individual cranes, but are committed to a larger goal (long term preservation of the gene pool).

In 1992, global priorities for captive propagation of all cranes were established as part of a **Conservation Assessment and Management Plan** (CAMP) which summarized management in the wild, recovery/management plans, research, and the size and type of captive programs needed to support field efforts.

At a Global Captive Action Plan (GCAP) workshop for cranes in 1993, the status of captive populations was examined including estimates of global and regional population sizes, degree of difficulty in breeding, existence of international or regional studbooks or management programs, and release programs. Topics examined included management of founders, research needs, studbook and management program needs, and methods for coordinating global and regional programs. Target populations were established for the world.

Regional crane **Taxon Advisory Groups** (TAGs) are being formed to determine regional roles in captive management, coordinate allocation of limited space and resources between taxa, and coordinate programs with other regions. Crane TAGs have been established for global populations in North America, Europe, Africa, and Australia (see Table 9.3). Chinese and Japanese TAGs are being developed.

Global cooperation for individual species is organized under Global Animal Survival Plans (GASPs). Some species, such as the Red-crowned Crane, can be effectively managed as regional metapopulations with periodic exchange of bloodlines. Other species, such as the Siberian Crane, have a lower number of founders and must be managed globally to insure genetic health. GASP workshops have been held for the Red-crowned and Siberian Cranes and are recommended for the Black-necked, Hooded, White-naped, and Wattled Cranes.

<sup>&</sup>lt;sup>2</sup> Adapted from Wiese and Willis (1993).

#### **TABLE 9.3.**

#### Summary of studbooks and management programs for cranes.

#### Regional Taxon Advisory Group (TAG) Coordinators for C ranes

Conservation Breeding Specialist Group (CBSG)

Captive Crane Working Group:

Claire Mirande, International Crane Foundation

North America:

Claire Mirande, International Crane Foundation

Gunter Schleussner, Wilhelna Zoological Gardens

U.K. and Ireland:

Nick Lindsay, Whipsnade Zoo, and Dave Coles, Child Beale Trust

Alan Abrey, Umgemi Bird Park

China:

To be determined

Japan:

Kazuaki Nippashi, Saitama Children's Zoo

#### White-naped Crane

International Studbook Keeper and SSP

(North America) Coordinator:

Christine Sheppard, Wildlife Conservation Society

EEP (Europe) Coordinator:

Peter Muhling, Nuremberg Zoo

JMSC (U.K.) Studbook Keeper:

Nick Lindsay, Whipsnade Zoo

SSCJ (Japan) Coordinator, Studbook Keeper and Regional Coordinator:

Kazuaki Nippashi, Saitama Children's Zoo

#### Wattled Crane

International Studbook Keeper and SSP Coordinator: Fred Beall, Franklin Zoological Park

Global Animal Survival Plan (GASP) Coordinators: Fred Beall, Franklin Zoological Park Linda Rodwell, The Highlands Crane Group

JMSC Studbook Keeper and JMSP Coordinator: Nick Lindsay, Whipsnade Zoo

SSCJ Studbook Keeper and Coordinator: Masanori Kobyashi, Chiba Zoo

#### **Hooded Crane**

International Studbook Keeper and SSP Coordinator: Bruce Bohmke, Phoenix Zoo

JMSC Studbook Keeper and JMSP Coordinator: Nick Lindsay, Whipsnade Zoo

SSCJ Studbook Keeper & Regional Coordinator: Takeshi Sakoh, Hira Kawa Zoo

#### Siberian Crane

International Studbook Keeper and International Global Animal Survival Plan (GASP) Coordinator:

Vladimir Panchenko, Oka State Nature Reserve, Lakash

Chinese Studbook Keeper:

Zhao Qingguo, Chinese Association of

Zoological Gardens

#### Red-crowned Crane

Global Animal Survival Plan:

no coordinator designated

International Studbook Keeper and SSCJ Coordinator: Teruyuki Komiya, Tokyo Ueno Zoo

North American Studbook Keeper:

Scott Swengel, International Crane Foundation

SSP Coordinator:

Claire Mirande, International Crane Foundation

Chinese Studbook Keeper and Regional Coordinator: Liu Dajun, Shenyang Zoo

EEP Coordinator and Regional Studbook Keeper: Rob Belterman, Rotterdam Zoo

JMSC Studbook Keeper and JMSP Coordinator: Nick Lindsay, Whipsnade Zoo

#### Blue Crane

International Studbook Keeper:

Ferdi Schoeman, National Zoological Gardens of South Africa

North American Studbook Keeper:

Susan Scott, North Carolina Zoological Park

JMSC Studbook Keeper and JMSP Coordinator: Whipsnade Zoo

#### West African Crowned C rane

North American Studbook Keeper: Susan Haeffner, Denver Zoo

IMSC Studbook Keeper:

Roger Wilkinson, Chester Zoo

#### Black-necked Crane

Chinese Studbook Keeper:

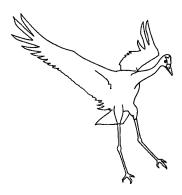
Zhao Qingguo, Chinese Association of Zoological Gardens

Sample studbook produced by SPARKS software.

M 19 May 84 M 26 May 84 F 18 Jun 84 M 20 Jun 84		Call	Location	Date	Local ID	Event	Birth/Origin	Death Date	Rearing	Name
	84 UNK	4	Baraboo	19 May 84	910-9	Hatch	Captive Born		Hand	A. Wright
	.84 I8	+	Baraboo	26 May 84	6-017	Hatch	Captive Born		Hand	Avery
				25 Sep 87		Death		25 Sep 87		
	84 5	12	Baraboo	20 Jun 84	6-018	Hatch	Captive Born		Hand	Dr. Saab
		4	Baraboo	20 Jun 84	6-019	Hatch	Captive Born		Hand	Ferguson
			Walsrode	16 Mar 88	UNK	Transfer				
M to Jun 85	85 18	4	Baraboo	ro Jun 85	6-020	Hatch	Captive Born		Hand	Gole
			Tokyotama	12 Mar 86	UNK	Transfer				
M 20 Jun 85	85 5	12	Baraboo	20 Jun 85	6-021	Hatch	Captive Born		Hand	Samar
			Tokyotama	12 Mar 86	UNK	Transfer				
F 17 May 86	8I 98	4	Baraboo	17 May 86	6-022	Hatch	Captive Born		Hand	Ranjit
M 27 May 86	8I 98	4	Baraboo	27 May 86	6-023	Hatch	Captive Born		Hand	Leif
				27 Nov 90		Death		27 Nov 90		
86 nn 77 Jun 86	86 43	12	Baraboo	17 Jun 86	6-024	Hatch	Captive Born		Hand	Spitzin
				21 May 88		Death		21 May 88		
M 2 Jul 86	9. Wild	Mild	Oka	2 Jul 86	OKA-30	Hatch	Captive Born		Hand	Kieng
F 3 Jul 86	9 Wild	Mild	Oka	3 Jul 86	ОКА-31	Hatch	Captive Born		Hand	Banyl
F 3 Jul 86	9 Wild	Mild	Oka	3 Jul 86	OKA-32	Hatch	Captive Born		Hand	Igel
				7 Aug 86		Death		7 Aug 86		
M 3 Jul 86	9 Wild	Mild	Oka	3 Jul 86	OKA-33	Hatch	Captive Born		Hand	Kulumer
			Moscow	13 Oct 86	UNK	Transfer				
				24 Nov 86		Death		24 Nov 86		
M 4 Jul 86	9. Wild	Mild	Oka	4 Jul 86	OKA-35	Hatch	Captive Born		Hand	Uol
				30 Jul 86		Death		30 Jul 86		
M 4 Jul 86	9. Wild	Mild	Oka	4 Jul 86	OKA-34	Hatch	Captive Born		Hand	Kjuel
				3 Nov 86		Death		3 Nov 86		

Species management programs have been formed for regional coordination of captive management including recommendations for transfers, pairings, and pair-by-pair productivity. Table 9.3 summarizes management programs for cranes.

The Population and Habitat Viability Analysis (PHVA) process uses computer simulation modelling (VORTEX software) to predict the probability of survival or extinction of wild and captive populations under current and potential conditions. PHVAs are a valuable tool in the development of recovery plans. Workshops have been held for Whooping, Redcrowned, Siberian, Mississippi Sandhill, and Wattled Cranes. For information contact: Conservation Breeding Specialist Group (CBSG) (address in Appendix) or Claire Mirande at ICF.



## Genetic Research

#### Significance

Studies of genetic diversity and relatedness are particularly relevant to management of species such as the Whooping Crane where the captive flock was established from a very small wild population (i.e., following a genetic bottleneck). Although eggs from this population were collected from known nest sites, the relatedness of wild pairs and the continuity of nest site use are unknown (Gee et al. 1992). Diversity can also be used to evaluate divergence between populations important for setting management goals. For example, we need to know how much the Mississippi Sandhill Crane differs from the other Sandhill subspecies to evaluate our investment in its preservation.

Accurate pedigree information is essential for genetic management. Unfortunately, parentage is unknown in some captive cranes (either because

semen from more than one donor has been used to inseminate a female or because more than one female occupies the pen where an egg is found). Sometimes poor record keeping clouds parentage information.

#### **Ongoing Genetic Research**

Research on diversity and relatedness in cranes encompasses many techniques including protein electrophoresis, restriction fragment length polymorphisms (RFLP), competitive binding immunoassays, and blood typing. Details on these techniques are presented by Gee et al. (1992).

Protein electrophoresis reveals a small part of the entire genome by examining blood or tissue homogenates for banding patterns associated with specific enzymes. These bands represent phenotypes at the enzyme locus. This gives information on the number of alleles segregating at the locus in a population and the genotypes of the individuals tested (Gee et al. 1992). Early work with electrophoresis on cranes by Morgan, at the University of Maryland in 1975, indicated a limited amount of variation.

A recent technique in DNA analysis or genetic fingerprinting examines variations in DNA structure (Jeffries et al. 1985; Vassart et al. 1987). Enzymes (restriction endonucleases) are used to cleave DNA. The resulting fragments contain tandemly repeated sequences that are highly polymorphic (RFLP). Radiolabelled complementary probes have been developed to identify these fragments, providing fingerprints that are unique to each individual tested. These fingerprints provide an excellent means for identifying relatedness between individuals and to estimate population diversity (Jeffries et al. 1991; Gever et al. 1993).

Several RFLP studies were conducted on cranes. Longmire et al. (1992) used a species-specific probe developed from Whooping Crane red blood cell DNA to examine relatedness and diversity in this species. Love and Dessauer used a species-specific probe to examine differences between Whooping Cranes and other closely related species (Love 1990). RFLP techniques have also provided a new technique for sexing cranes by developing a probe to identify repeat sequences characteristic to the W chromosome (see Chapter 11C).

Competitive binding immunoassays use a labelled antibody or antigen to detect immune reactions characteristic of individuals or groups of animals. Although this technique has been successfully used in

other species, attempts on cranes have proven unsuccessful to date (Gee et al. 1992).

Blood typing of the Major Histocompatibility Complex (MHC) is being used to determine relatedness and diversity in cranes. In this technique, antibodies are used to identify antigens which are controlled by individual gene loci. These loci segregate independently and can be used to estimate heterozygosity and relatedness.

Work is being conducted by W. E. Briles of Northern Illinois University, M. M. Miller at the Beckman Research Institute, and S. I. Jarvi at the Smithsonian Institution on the MHC in cranes (Jarvi et al. 1992). By absorbing (treating) known chicken specific reagents with the blood of a crane, it is now possible to prepare reagents capable of detecting individual forms of the MHC in a species of interest. Patuxent is collaborating to develop crane specific reagents using Sandhill Cranes. This study has been able to help elucidate the paternity of individual cranes. M. M. Miller is conducting molecular analysis of the MHC utilizing chicken MHC chromosomal DNA probes and developing additional species-specific probes through polymerase chain reaction and cloning techniques.

Information is also being collected on the relationship between MHC diversity and disease resistance (Allan and Gilmour 1962; Benacerraf 1981; Briles et al. 1983). MHC molecules bind antigens and activate the T cell response to foreign pathogens (Kurlander et al. 1992) playing an important role in the immune response. Maintaining MHC diversity may play a significant role in the survival of some endangered cranes. Breeding objectives based on MHC should be carefully integrated into strategies for maintaining genetic diversity across the entire genome (see Tables 9.1 and 9.2; Hughes 1991).

supported the morphological and behavioral classification of 15 crane species. Allozyme analysis allowed genetic diversity estimates for Sandhill, Sarus, Siberian, and Whooping Cranes (Dessauer et al. 1992). Krajewski (1988), using DNA-DNA hybridization, found one group of five species so closely related that they could not be differentiated. In a later study, he separated the group into 5 distinct species using a highly polymorphic region of mtDNA (Krajewski and Fetzner 1994). Krajewski is also using mtDNA to evaluate the relationship of crane subspecies. Sheri Snowbank at Southern Illinois University is using mtDNA to determine maternal linages of Whooping Cranes which survived the 1942 population bottleneck. Also, Travis Glenn at the Smithsonian Institution is using microsatellite DNA fingerprinting (RFLP) in museum specimens to estimate Whooping Crane genetic diversity before the 1942 bottleneck. Future research needs include continued examination of relatedness of wild caught birds, completion of paternity analysis, and refinement and application of MHC studies.

Lastly, genetic research can reveal taxonomic rela-

tionships. DNA-DNA hybridization (Sibley and

Ahlquist 1983) and allozyme (Ingold 1984) studies

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